Asynchronous Eye Closure as an Anti-Predator Behavior in the Western Fence Lizard (*Sceloporus occidentalis*)

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Abstract

Asynchronous eye closure (ASEC), one eye open while the other is closed, is a behavior observed in birds, some aquatic mammals, and reptiles. In birds and aquatic mammals, ASEC is associated with unihemispheric sleep wherein the cerebral hemisphere contralateral to (i.e. neurologically connected to) the closed eye sleeps while the other cerebral hemisphere remains awake with its associated eye open and functional. Evidence from birds suggests that ASEC is an important anti-predator adaptation to mediate the trade-off between the need to remain vigilant and the need to sleep. However, the anti-predator correlates of ASEC remain largely unstudied in other animals. Here, we present behavioral evidence that ASEC in reptiles is also an anti-predator adaptation used in response to an increase in the risk of predation. ASEC was measured in captive western fence lizards (*Sceloporus occidentalis*) individually exposed to three experimental treatments: (1) an empty terrarium, (2) a terrarium housing a novel moving object, and (3) a terrarium housing a live predator (snake). Predator exposure elicited significantly higher levels of vigilance, mostly due to an increase in ASEC. This increase in ASEC came largely at the expense of synchronous eye closure (both eyes closed). Lizards in ASEC also showed a strong tendency to orient their open eye in the direction of the predator. We suggest that lizards engaged in ASEC are sleeping unihemispherically and are thus able to maintain a level of vigilance concurrent with sleep.

Introduction

Levels of awareness about the external environment occur along a continuum from deep sleep to alert wakefulness. Based upon behavioral criteria, sleep is characterized by inactivity and decreased responsiveness to stimuli (Piéron 1913; Flanigan 1972). A sleeping animal is thus highly vulnerable to predation (Lima et al. in press). Some animals, however, have evolved mechanisms to resolve this fundamental conflict between the need to remain vigilant and the need to sleep. Virtually all birds and some aquatic mammals engage in unihemispheric sleep, a sleep state in which one half of the brain sleeps while the other remains awake to some extent (Rattenborg et al. 2000). Specifically, the cerebral hemisphere contralateral to (i.e. neurologically connected to) the open eye maintains an electrophysiological brain wave pattern indicative of wakefulness, while the hemisphere contralateral to the closed eye exhibits a pattern typical of sleep. Therefore, the closure of one eye while the other remains open, also known as asynchronous eye closure, is a behavioral correlate of unihemispheric sleep (Rattenborg et al. 2000; Lyamin et al. 2004).

Extant reptiles may also engage in unihemispheric sleep (Rattenborg et al. 2000; Lesku et al. in press). Lizards may exhibit any one of three mutually exclusive eye states: (1) synchronous eye opening (i.e. wakefulness), (2) synchronous eye closure (both

eyes closed), a behavior associated with sleep when exhibited in conjunction with prone body postures (Flanigan et al. 1973; Meglasson & Huggins 1979; Ayala-Guerrero et al. 1988), and (3) asynchronous eye closure (ASEC). ASEC appears to be taxonomically widespread among reptiles, having been observed in crocodilians (Warner & Huggins 1978), turtles (Flanigan et al. 1974) and tortoises (Flanigan 1974), and lizards (Tauber et al. 1966, 1968; Flanigan 1973; Mathews & Amlaner 2000); however, this behavior has been quantified only for the western fence lizard (*Sceloporus occidentalis*; see Mathews & Amlaner 2000). Furthermore, no study has yet examined the adaptive significance of ASEC in reptiles. Consequently, it is currently unknown whether reptilian ASEC reflects unihemispheric sleep, or more generally an anti-predator adaptation.

Following a strictly behavioral definition of sleep (see Flanigan 1972), ASEC may not seem to qualify as a form of sleep in *S. occidentalis* as arousal thresholds are not elevated during ASEC compared with synchronous eye opening (Mathews & Amlaner 2000). Yet this result does not preclude an association between ASEC and some form of sleep in reptiles. In mallard ducks (*Anas platyrhynchos*), arousal thresholds during ASEC are also very low despite conclusive electrophysiological evidence that the ducks are indeed sleeping unihemispherically (Rattenborg et al. 1999a,b).

There are, however, non-sleep-related hypotheses for the adaptive significance of reptilian ASEC. For example, some suggest that eye closure in reptiles serves to reduce evaporative water loss from the eyes (Kavanau 1997; Lanham & Bull 2004). In birds, there is some evidence that ASEC may protect the eyes from asymmetrical environmental influences, such as directional sunlight (Ball et al. 1985), which may also apply to reptiles. Alternatively, as animals have a finite amount of attention to devote to vigilance (Dukas 2004), ASEC in an animal with laterally placed eyes may focus the animal's attention on a clear threat by eliminating the superfluous portion of the visual field.

We hypothesize that ASEC in *S. occidentalis* represents an anti-predator behavior. Therefore, we predict that the use of ASEC should be sensitive to changes in the local risk of predation (Lima & Dill 1990; Lima et al. in press). Specifically, the percentage of time devoted to ASEC should increase with a heightened perception of predation risk. Furthermore, the open eye during ASEC should be strongly directed towards the perceived threat, as has been demonstrated in birds (Rattenborg et al. 1999a,b). A second prediction, not specific to ASEC, is that visual scanning should increase following an increase in the risk of predation (Lima & Dill 1990), as has been observed in birds and mammals (Elgar 1989; Hankerson & Caine 2004), and more recently in reptiles (Lanham & Bull 2004). We tested these predictions by recording the responses of individual lizards to a nearby predator, a live black rat snake (*Elaphe obsoleta*), and compared these responses to those observed in two different control treatments.

Methods

Eight adult western fence lizards (two male, six female) were wild-caught in Texas, USA and obtained from the Charles D. Sullivan Company (Nashville, TN, USA). Lizards were housed individually in 38 l (60 × 32 × 30 cm) terraria with potting soil substrate. Illumination during the light phase of the photoperiod was provided by 10 40-W fluorescent light bulbs mounted on the ceiling. All lizards were maintained on a 12 : 12 h light : dark cycle at 30 : 22°C, and provided crickets (*Acheta domestica*) and water ad libitum. This diet was supplemented weekly by dusting crickets with multi-vitamins. The black rat snakes (76–120 cm shout-vent length (SVL)) used as predators were captured in the Ouachita National Forest (Hot Springs, AR, USA). Snakes were maintained in 38 l (60 × 32 × 30 cm) terraria with cedar chip substrate and were fed mice biweekly with water available ad libitum. Although black rat snakes are not a natural predator of the western fence lizard, other species of snakes are certainly important predators of *S. occidentalis* (Fitch 1940), and it is likely that these lizards perceive all snakes, when detection is based solely upon visual cues, as a potential threat. All experimental procedures were conducted under an approved animal care and use protocol (ISUIACUC 96 CA/CM).

Experiments were conducted between 11:00 and 14:00 hours in a 5 × 3 m recording room kept at 25°C. During each experimental trial, a lizard was removed from its home terrarium and placed in an 8 × 16 × 12 cm transparent plastic terrarium to facilitate video recordings. At this time, a small amount of commercially available white make-up cream (non-toxic, water-based) was applied to the outside of the lizard's eyelids to facilitate eye state determination from the video recordings. This technique has been used successfully in a previous study (Mathews & Amlaner 2000) and had no apparent effect on the lizard's eye state. A 2.4 × 1.5 m area in the center of the recording room contained four recording areas

arranged in a 2 × 2 array, each containing a single plastic terrarium and four small video cameras, one facing each side of the lizard's terrarium, to record lizard eye state. Brown cardboard (80 × 40 cm) was placed between adjacent terraria to visually isolate each recording area from the other three. Each recording area also contained a 38-l presentation terrarium placed 25 cm from the lizard's terrarium. The contents of this presentation terrarium were concealed from the lizard by a removable 34 × 60 cm panel of brown cardboard. A lizard was placed in its terrarium at least 4 h prior to recording. Lizard behavior (eye state) was recorded on a Panasonic video recording system utilizing two eight-channel digital sequential frame switchers and two VCRs. This 16-camera system allowed simultaneous video recording of all four lizards at a temporal resolution of 0.27 s between images taken by an individual camera.

This study utilized three experimental treatments. One treatment consisted of a 38-l presentation terrarium containing only wood chips and a filled water bowl (empty control). This treatment controlled for the sudden appearance of the terrarium itself and the experimenter's brief presence in the room (see below). A second control treatment consisted of a novel moving object (moving control). This treatment was set up as in the empty control with the addition of a 7 × 6 × 2 cm block of gray foam, with a magnet embedded inside, set horizontally on top of a magnetic stir plate. The foam block rotated on the stir plate at approx. 160 rpm and exposed each lizard to a novel moving stimulus. The predator exposure treatment consisted of a terrarium (set up as in the empty control), containing a live black rat snake. Each snake was stimulated to move by touching it with an aluminum pole immediately before its presentation to the lizard. Sham stimulations (moving the aluminum pole) were also applied during the other two treatments to control for the possible effect of the experimenter's brief presence in the room. All snakes moved slowly across the bottom of the terrarium for up to several minutes before ceasing motor activity.

In all treatments, the contents of a presentation terrarium were in view to a lizard only after the experimenter entered the recording room and removed the cardboard divider between the lizard and the terrarium. After removing the cardboard dividers, the experimenter promptly left the recording room. The contents of the presentation terrarium were visible for 10 min, after which the experimenter re-entered the recording room, replaced the card-

board divider, and again immediately exited the recording room.

Lizards underwent experimentation in two groups of four animals. Each member of a group was subjected to one of the control treatments on the first round of trials, with half receiving the empty control (n = 4) and half receiving the moving control (n = 4). The first control was followed by a round in which all subjects received the predator exposure treatment. Predator exposure was followed by a final round of control treatments in which each lizard received the control treatment not experienced in the first round of trials.

Using the video recordings, lizard eye state was scored as synchronous eye opening (SEO), asynchronous eye closure (ASEC), or synchronous eye closure (SEC) every second for 3-min blocks of time for four different sample periods: (1) 20 min before the start of a presentation (BEFORE), (2) immediately after the presentation (AFTER:0), (3) 15 min after the presentation (AFTER:15), and (4) 30 min after the presentation (AFTER:30). To quantify the amount of visual scanning of the environment, an Index of Vigilance was calculated as:

$$\text{Index of Vigilance} = 2(\%\,\text{SEO}) + (\%\,\text{ASEC})$$

where % SEO and % ASEC are the percentage of each sample period devoted to the indicated eye state. In the above equation, SEO is given twice the weighting of ASEC as a lizard with both eyes open can scan about twice the area that can be scanned during ASEC (given the lateral placement of eyes). SEC was omitted from this calculation (i.e. given a weighting of zero) because during this eye state animals are unresponsive to visual stimulation and are therefore considered to be non-vigilant.

Statistical analyses were performed in Systat 10 (SPSS, Chicago, IL, USA) using two-way repeated-measures analysis of variance (ANOVA). Individuals, treatment, and time were treated as independent variables along with a dependent variable of: (1) Index of Vigilance, (2) % ASEC, (3) % SEC, or (4) % SEO. Two-tailed Wilcoxon signed rank tests were used to determine significance of eye state orientation (i.e. if the animal's eye was preferentially directed towards or away from the last known location of the predator). Sample size (n) indicates the number of lizards for which a statistical comparison could be made. Data from one lizard were omitted from the analysis of the predator exposure treatment for all samples after the presentation, and data from a second lizard were removed from the analysis of the moving control treatment for the

AFTER:15 and AFTER:30 sample because of a procedural mishap.

Results

The Index of Vigilance (Fig. 1a) varied significantly across treatments (Table 1a; p < 0.001) and varied significantly across time (p < 0.001), but did not vary significantly between individuals (p = 0.114). The interaction between treatment and time was significant (Table 1a; p = 0.007). Visual inspection of Fig. 1a reveals that the relative increase in the Index of Vigilance was clearly greatest immediately following predator exposure and remained somewhat elevated post-presentation.

The use of asynchronous eye closure (ASEC; Fig. 1b) varied significantly across treatments (Table 1b; p < 0.001) and varied significantly across time (p = 0.004), but did not vary significantly between individuals (p = 0.790). The effect of time was dependent upon treatment (Table 1b; p = 0.046). For the predator exposure treatment, ASEC significantly increased immediately following predator exposure (paired t-test: t = −3.384, df = 7, p = 0.012; Fig. 1b) and remained significantly eleva-

ted 15 min post-presentation (t = −3.573, df = 7, p = 0.009; Fig. 1b), but was no longer significantly elevated 30 min post-presentation (t = −1.037, df = 7, p = 0.334; Fig. 1b). The observed pattern in ASEC is basically the same as that seen in the Index of Vigilance (Fig. 1a), indicating that the increase in vigilance following predator exposure was primarily due to an increase in ASEC. ASEC also significantly increased immediately following presentation of the empty control (t = −3.012, df = 7, p = 0.020; Fig. 1b), but not immediately following presentation of the moving control (t = −1.498, df = 7, p = 0.178; Fig. 1b).

Expressed as the percentage of total ASEC in which the open eye was directed toward the presentation terrarium (Fig. 2), the open eye was oriented significantly towards the presentation terrarium following the predator exposure treatment (Wilcoxon signed rank test: n = 5, Z = −2.023, p = 0.043), but not after the empty control (n = 5, Z = −1.214, p = 0.225) or moving control (n = 7, Z = 0.338, p = 0.735) treatments. Directional orientation of ASEC was analyzed only for BEFORE and AFTER:0 comparisons. During ASEC, the orientation of the open eye could be determined only for five animals
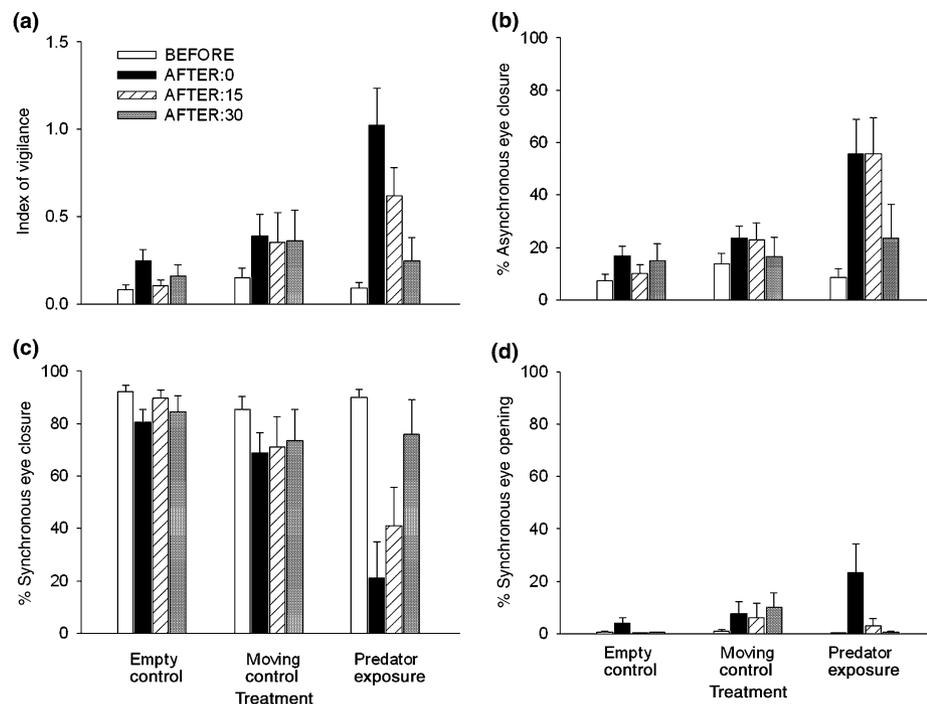

Fig. 1: Temporal course of (a) the Index of Vigilance, (b) asynchronous eye closure (ASEC), (c) synchronous eye closure (SEC), and (d) synchronous eye opening (SEO). Data are shown for the empty control, moving control, and predator exposure treatments across the following time periods: 20 min before the start of a presentation (BEFORE; open), immediately after the presentation (AFTER:0; filled), 15 min after the presentation (AFTER:15; hatched), and 30 min after the presentation (AFTER:30; gray). Presented values are mean ± SE

Dependent variable	Source	SS	df	MS	F-ratio	p-value
(a) Index of Vigilance	Individual	1.254	7	0.179	1.732	0.114
	Treatment	1.919	2	0.960	9.274	<0.001
	Time	2.524	3	0.841	8.132	<0.001
	Treatment * Time	2.012	6	0.335	3.241	0.007
	Error	7.760	75	0.103		
(b) Asynchronous eye closure	Individual	1967.685	7	281.098	0.554	0.790
	Treatment	9478.261	2	4739.130	9.347	<0.001
	Time	7478.349	3	2492.783	4.916	0.004
	Treatment * Time	6892.770	6	1148.795	2.266	0.046
	Error	38027.053	75	507.027		
(c) Synchronous eye closure	Individual	5875.961	7	839.423	1.317	0.254
	Treatment	14278.200	2	7139.100	11.201	<0.001
	Time	13941.419	3	4647.140	7.291	<0.001
	Treatment * Time	11781.087	6	1963.514	3.081	0.009
	Error	47801.720	75	637.356		
(d) Synchronous eye opening	Individual	1526.532	7	218.076	1.676	0.128
	Treatment	552.317	2	276.158	2.123	0.127
	Time	1697.185	3	565.728	4.348	0.007
	Treatment * Time	1647.569	6	274.595	2.110	0.062
	Error	9758.226	75	130.110		

Table 1: Results of repeated-measures anovas for Index of Vigilance, asynchronous eye closure, synchronous eye closure, and synchronous eye opening
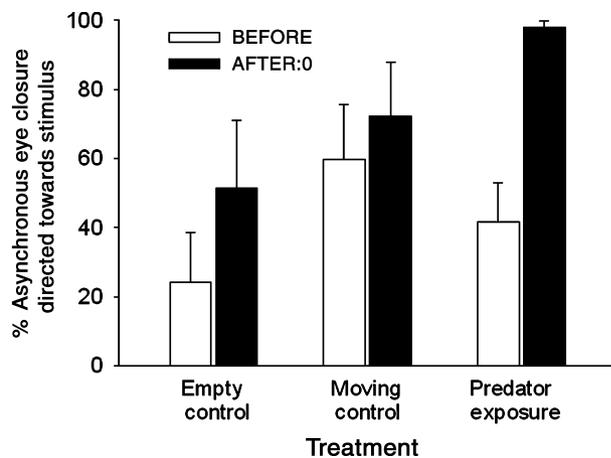

Fig. 2: Percentage of asynchronous eye closure (ASEC) in which the open eye was directed toward the presentation terrarium for the empty control, moving control, and predator exposure treatments. Comparisons of the directional orientation of ASEC are made only between the 3 min sampling epochs of the BEFORE (20 min before the start of a presentation) and AFTER:0 (immediately following the presentation) time periods. Presented values are mean ± SE

in the empty control and predator exposure treatments, and for seven animals in the moving control treatment, as some lizards directly faced the stimulus terrarium making impossible a directional determination of ASEC.

Synchronous eye closure (Fig. 1c) varied significantly across treatments (Table 1c; p < 0.001) and varied significantly across time (p < 0.001), but did not vary significantly between individuals (p = 0.254). The effect of time was dependent upon treatment (Table 1c; p = 0.009). The observed pattern in synchronous eye closure is essentially the inverse of that seen in the ASEC data (Fig. 1b), indicating that the increase in ASEC came at the expense of synchronous eye closure. Accordingly, synchronous eye opening (Fig. 1d) did not differ significantly across treatments (Table 1d; p = 0.127) or between individuals (p = 0.128), but did vary significantly across time (p = 0.007); the effect of time reflects a tendency for an increase in synchronous eye opening immediately following stimulus presentation. The interaction between treatment and time was marginally nonsignificant (Table 1d; p = 0.062).

Discussion

Both predictions generated by the anti-predator hypothesis for reptilian ASEC were supported by the results. The large increase in visual scanning following predator exposure supports our prediction that lizards should respond to a heightened risk of predation with increased vigilance. The percentage of time devoted to ASEC increased with heightened risk of predation and the open eye was oriented toward the perceived threat. Synchronous eye closure was greatly reduced following predator exposure, whereas synchronous eye opening was relatively unaffected by treatment. Therefore, the increase in vigilance following predator exposure was not due

to an increase in synchronous eye opening, but rather to an increase in ASEC at the expense of synchronous eye closure. The results also suggest that the lizards perceived the snakes as a genuine threat, even though black rat snakes are not a natural predator of the western fence lizard. Specifically, the generally minimal response to the moving control treatment suggests the lizards did not simply perceive the moving snake as a 'novel object', but rather as a predator.

Our results on overall vigilance are similar to those found by Lendrem (1984), who reported increased visual scanning in sleeping barbary doves (*Streptopelia risoria*) after a simulated predator encounter in the laboratory, and by Gauthier-Clerc et al. (1998) who reported a similar response in sleeping green-winged teal (*Anas crecca*) after exposure to a natural predator in the field. In another study, ducks sleeping in the center of a linear group engaged predominantly in bihemispheric sleep (i.e. the form of sleep typical of terrestrial mammals), whereas ducks sleeping at the periphery of the group engaged in 150% more unihemispheric sleep (Rattenborg et al. 1999a,b). This suggests that bihemispheric sleep is more efficient at achieving sleeps' restorative functions, and that unihemispheric sleep reflects a compromise between the physiological need to sleep and the ecological demands of predator detection.

Our results indicate that the overall increase in vigilance during the predator exposure treatment was primarily because of a large increase in ASEC at the expense of synchronous eye closure, but why did the lizards not respond to the predator by opting to open both eyes? One hypothesis for eye closure in reptiles posits that eye closure reduces evaporative water loss from the eyes (Kavanau 1997; Lanham & Bull 2004). ASEC may indeed reduce water loss, but this hypothesis cannot explain the observed increase in ASEC following the sudden appearance of a predator. Moreover, this increase in ASEC came at the expense of synchronous eye closure and not synchronous eye opening. A second, non-sleep-related hypothesis might be that since attention is a finite resource (Dukas 2004), lizards may close one eye to better focus their limited attention toward a clear and present threat. Thus, lizards would restrict their visual field to occlude stimuli from the eye not directed toward the predator. Although this hypothesis can explain why our lizards increased their use of ASEC following predator exposure and why they preferentially closed the eye facing away from the predator, it cannot explain why the large increase in

ASEC came at the expense of synchronous eye closure and not synchronous eye opening. We suspect that, as in birds and aquatic mammals, *Sceloporus occidentalis* also gains some of the benefits of sleep while engaging in ASEC.

The precise functions of sleep are unknown (Rechtschaffen 1998), but it appears that sleep is essential for survival (Rechtschaffen & Bergmann 2002; Shaw et al. 2002). This 'essential' nature of sleep undoubtedly applies to lizards and other reptiles, and the results of our study suggest that ASEC in reptiles represents an evolutionary compromise between the need to remain vigilant and the need to sleep. Furthermore, our results suggest that lizards are able to engage in unihemispheric sleep, but further behavioral and electrophysiological studies are needed to determine the validity of this assessment. Such an investigation may also yield much insight into the evolution of avian unihemispheric sleep (Rattenborg et al. 2000) and sleep in vertebrates in general (Rattenborg & Amlaner 2002; Lesku et al. in press).

Acknowledgements

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